Landscape level variation in tick abundance and red deer migration pattern

Nina Risnes Olsen

Master of Science thesis

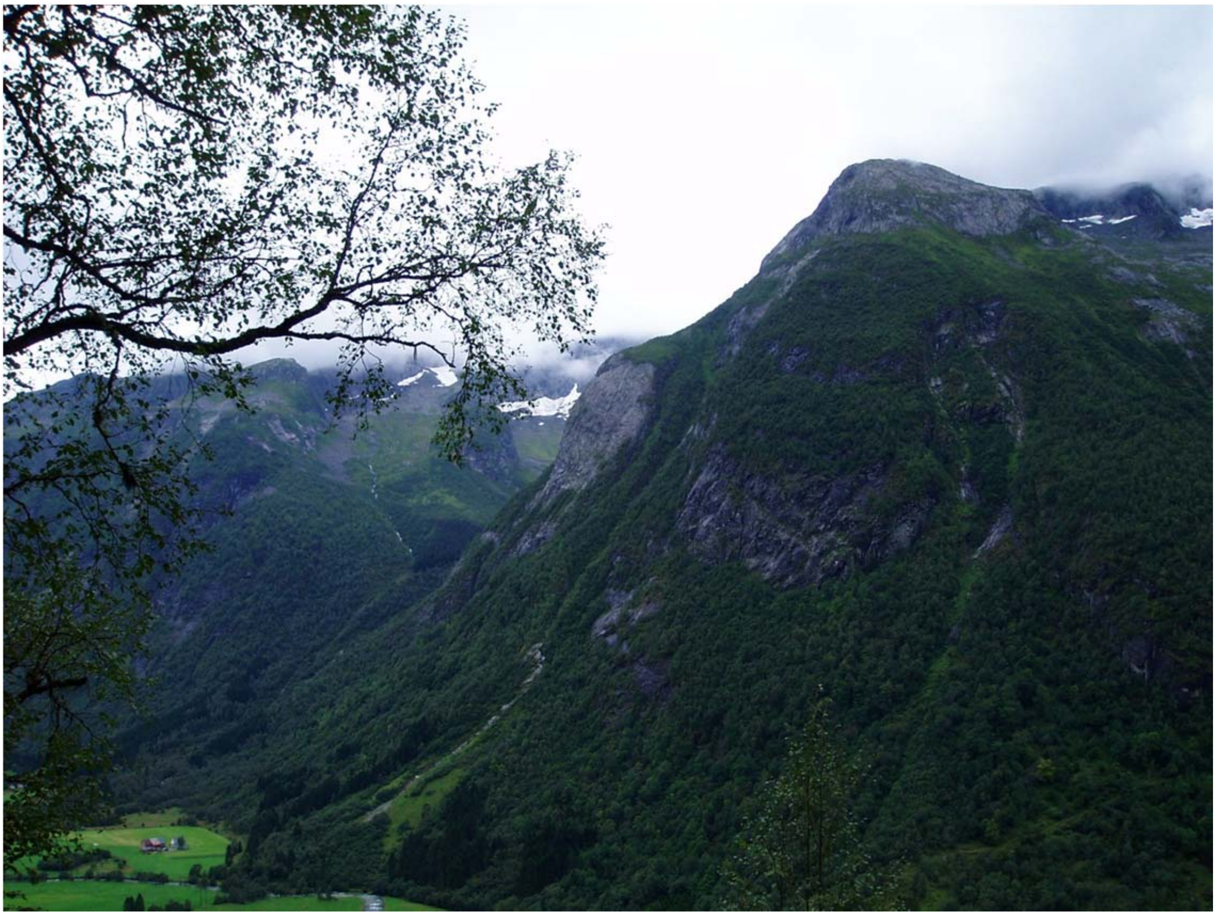
2011

Centre for Ecological and Evolutionary Synthesis

Centre for Ecological and Evolutionary Synthesis

Department of Biology

University of Oslo, Norway



Vetlefjorden in the county Sogn og Fjordane, Norway. Photo by Nina Risnes Olsen

Preface

This study was conducted at the University of Oslo, Norway, under the supervision of Atle Mysterud and Leif Egil Loe. I would like to thank my supervisors for great help and guidance during the past two years. Thank you for always being available and for answering my numerous questions. Many thanks go to Atle Mysterud for giving me the chance to write this master thesis and allowing me to experiencing fieldwork. Thank you for your quick response and great feedback. Many thanks go to Leif Egil Loe for all the help with ArcGIS.

Bjørnar Ytrehus and Hildegunn Viljugrein from the Norwegian Veterinary Institute, in addition to Reidar Mehl, also deserve big thanks for great collaboration in the initial phase of this thesis. Huge thanks go to Kim Magnus Bærum for helping me with the fieldwork.

Many thanks also go to my boyfriend for always being there for me and support me, and for keeping up with several tons of articles, books and other master-related things that have flooded our apartment these last years. My parents and my friends also deserve huge tanks for always being there to support me and drive me forward. Last but not least big thanks go to my dog for keeping me company out in the field and for always being able to get me in a good mood.

Nina,
Blindern, May 30th 2011

Jølstravatnet lake in Sogn og Fjordane. Photo by Nina Risnes Olsen

Abstract

Over the past decades the population of red deer, *Cervus elaphus*, along the south-west coast of Norway have increased 10 fold in density as evidenced from the harvest statistics. At the same time the abundance of *Ixodes ricinus* ticks have increased. The increase in tick abundance causes major concern for the welfare of both humans and wildlife, but we still know very little about ticks. Previous studies have found a positive association between tick- and red deer abundance. In addition, a negative association with altitude and distance from coast have also been documented for different tick species. In Norway tick abundance is an increasing problem. Still, there have been performed no study looking on which factors may explain the landscape level variation in tick distribution in Norway. Nor have any study investigated how the tick abundance is related to the space use patterns of red deer. Red deer at the west coast of Norway are known to show partial migration. Migration in red deer is assumed to be mainly related to differences in plant phenology induced by distance from the coast and altitude. However, also ticks likely show an uneven altitudinal distribution thus playing a yet unknown role in this migratory system. The aim of this thesis was first to quantify how tick abundance is related to factors such as time period, distance from coast and altitude, and second to quantify tick abundance at a landscape level relative to red deer migration pattern and local density of deer. To achieve this, tick abundance was surveyed by aid of the cloth lure method within winter and summer areas of stationary and migratory red deer during spring and fall 2009. A lower abundance of ticks with increasing altitude and distance from the coast was found. Surprisingly there were a negative relationship between tick abundance and red deer density. When looking on tick distribution relative to red deer migration pattern the density of ticks was higher in the home range of stationary deer relative to migratory deer. The smallest amounts of ticks were found in summer areas of migratory red deer. These findings gives support to the hypothesis that migration further away from the coast and to higher altitudes in the summer provide a benefit to red deer in terms of avoiding areas likely to yield heavy tick loads. This study thus give a better understanding of which factors influence the landscape level variation in tick distribution in Norway, and indicates that ticks may play a previous unknown role in the migration system of red deer.

Table of contents

1. Introduction

The abundance of several cervids has increased all over Europe (Gordon et al. 2004, Milner et al. 2006) and North America (McShea and Underwood 1997). A typical example of this is the Norwegian red deer, *Cervus elaphus* (Milner et al. 2006). From the harvest statistic it is evident that the populations of red deer along the south-west coast of Norway have increased 10 fold in density over the past 40 years (Statistics Norway, 2009). Red deer is a very important game species in Norway, with 37 700 red deer killed in the licensed hunting in 2009 (Statistics Norway, 2009). The county of Sogn og Fjordane have the highest number of harvested red deer in Norway. Earlier studies have reported density effects in body mass and ovulation rates of red deer hinds (Langvatn et al. 2004, Mysterud et al. 2001a), in addition to density effects on sex ratio with less male calves being born with high density (Mysterud et al. 2000). The lowering of body weight due to density is, to some extent countered by the changes in climate that have generally increased weights (Mysterud et al. 2001c). The role of parasites, though, for these density dependent reductions in performance is not known, neither how parasites might influence behaviour such as migration patterns in these cervids.

The abundance of ticks has increased over the last decades. Several studies report an increase in the *Ixodes ricinus* tick in Europe (Gilbert 2010, Scharlemann et al. 2008) and even more studies report an increase in *Ixodes scapularis*, a close relative of *I. ricinus*, in North America (LoGiudice et al. 2008, Ostfeld et al. 2006, Van buskirk and Ostfeld 1995) over the last years. Theories to explain this include, among other, a changing climate and an increase in host abundance (Scharlemann et al. 2008). Several studies (Gilbert 2010, Materna et al. 2008, Rand et al. 2003) have found a negative correlation between tick abundance and altitude. Lindgren et al. (2000) argues that ticks might spread to higher latitudes and altitudes as well as becoming more abundant in established regions as the climate become milder. In fact there is evidence of a shift in the vertical distribution. Materna et al. (2008) concluded that upper limit of *I. ricinus* have shifted from 700-800 m up to at least 1100 m above sea level during the last two decades in the Czech Republic and the distribution can have expanded as much as 17% from 2005 to 2008 in Britain (Scharlemann et al. 2008). This expansion of the distribution and increase in tick abundance has naturally led to a significant increase in tick borne diseases both in Europe and North America (Gilbert 2010, LoGiudice et al. 2008, Ostfeld et al. 2006, Lindgren et al. 2000 and see Scharlemann et al. 2008 for even more references). *I. ricinus* is the primary vector of several agents causing diseases such as Lyme borreliosis, tick-borne encephalitis, anaplasmosis and babesiosis which causes major concern for the welfare of both wildlife and humans.

I. ricinus has a quite long lifespan. Normally the tick completes its life cycle within 2-3 years, although it can take between 1 to 7 years in extreme cases (Materna et al. 2008). The life cycle consists of an egg, larvae, nymph and adult stage. Ticks quest for hosts mainly on lower vegetation. On the host the tick attach itself and start feeding blood from the host. When engorged the tick falls of, and after every meal ticks moult before making the transition to the next stage of the life cycle. Usually it takes the tick one year to complete each stage (Knap et al. 2009). After the adult female has engorged she will lay as many as 2000 eggs. The tick's lifespan is influenced by temperature and host availability, and humidity is very important for tick survival. In Norway red deer is an important host for nymphs and adults (Rosef et al. 2009, 2008). Studies done by Rosef et al. (2009, 2008) and Matuschka et al. (1993) have shown that deer may be important reservoirs for *Anaplasma phagocytophilum* but incompetent carriers for *Borrelia burgdoferi s.l.* and thereby contribute to reducing the infection rate of Lyme disease on questing *I. ricinus* ticks. Small rodents are known to serve as the main hosts for the immature stages of *I. ricinus* (Rosef et al. 2008).

Currently there have been performed no study on how the distribution of ticks are related to the local distribution of red deer. Red deer at the west coast of Norway are known to show partial migration, thus not all deer migrate (Mysterud et al. 2011, Albon and Langvatn 1992). Stationary red deer is usually located at lower altitudes and closer to the coast than deer that migrate. For red deer, migration starts in spring and deer can migrate as far as 150km to summer areas that are located further inland and at higher altitudes than the winter areas which they migrate back to in late summer or fall (Langvatn and Albon 1986). Migration in red deer is assumed to be mainly related to differences in plant phenology induced by distance from the coast and altitude, in addition to snow avoidance in fall (Mysterud et al. 2011, Mysterud et al. 2001b, Albon and Langvatn 1992, Langvatn and Albon 1986). A recent study by Mysterud et al. (2011) has reported that migration also may be related to density of red deer in the area. Recent studies done in Scotland (Gilbert 2010, Ruiz-Fons and Gilbert 2010) have found a positive relationship between tick and deer abundance. Still, no one has yet considered parasite-avoidance as a possible contributing factor to the movement patterns of red deer and there are few accounts even for other ungulates. The exception is ectoparasites on reindeer that have been studied quite a lot (e.g. Rødven et al. 2009, Fauchald et al. 2007, Colman et al. 2003, Hagemoen and Reimers 2002, Toupin et al. 1996, Helle et al. 1992, Folstad et al. 1991). One of the aims of this study is therefore to investigate whether parasitism by ticks may give an additional benefit to migratory red deer.

In this study the aim is thus to first examine what kind of factors that causes landscape level variation in tick distribution on the west coast of Norway, and then estimate abundance of ticks relative to red deer migration pattern (known from an on-going marking study; Mysterud et al. 2011) and local red deer population density. Based on anecdotal evidence and previous studies, I predict a lower abundance of ticks with increasing altitude (P1) and distance from the coast (P2), that density of questing ticks will be higher in areas with a high (harvest) density of red deer (P3), and that tick abundance is higher in home ranges of stationary deer than in summer ranges of migratory deer (P4). I see it most likely that ticks will be present in both spring and in fall, but that there might be a smaller amount of ticks in fall.

2. Material and methods

2.1 Study area

The study area is located in the county of Sogn og Fjordane which lies in the western part of southern Norway (61°23′N 5°45′E). The transects sampled are located in the municipalities Flora, Naustdal, Jølster, Balestrand, Høyanger, Gaular, Askvoll, and Fjaler, and thus cover the majority of Sogn og Fjordane. The topography here is characterized by steep hills and mountains, fiords and valleys. The vegetation is mainly part of the boreonemoral zone and is dominated by deciduous- and pine forest, but there is also coastal heath in this region (Abrahamsen et al. 1977). This area typical has mild winters and relative warm summers. The outer and central coastal areas typically have an oceanic climate, while the inner fiords have a slightly continental climate that might lie in rain shadow (Abrahamsen et al. 1977). The west coast of Norway is generally characterized by heavy rainfall. Precipitation and temperature generally decline from coast to inland, while snow depth and duration of snow cover generally increases (Langvatn et al. 1996).

Figure 1. Overview of the study area in Sogn og Fjordane, Norway. The deer symbols illustrate the placement of transects surveyed in May and August 2009. To each transect one or several red deer home ranges are associated.

2.2 Sampling design

Ticks were sampled within summer and winter areas of migratory and stationary red deer based on data from GPS-marked individuals (marked in the period 2005 - 2007) (Mysterud et al. 2011). A transect was laid across each seasonal home range of all individuals. In several transects, though, the home range of more than one red deer was present along the transect. A total of 36 transects were drawn on maps based on available knowledge from GPS marked deer, of which 34 were used in the study. The last two transects was not usable in this study since one of them was situated in a housing area, and the second was situated in an extremely wet area. In addition, two red deer home ranges and two of the transects were excluded from the part of the analysis focusing on tick abundance in relation to red deer migration pattern and density of deer. One of the red deer home ranges was excluded because the deer showed a non-typical migration pattern and the other was excluded because it was unsure whether the deer migrated or not (see classification of deer in Mysterud et al. 2011). The two transects was excluded because they did not span any red deer home range.

Each transect was surveyed in spring (04.05.09 – 19.05.09) and fall/late summer (11.08.09 – 24.08.09). The period from May to August is regarded a crucial period for host finding and development for the *I. ricinus* since this is the period when the temperature increase is most pronounced as shown in the Czech Republic (Materna et al. 2008). The detailed activity pattern of ticks in Norway is to my knowledge not known. Still, it is likely to assume a similar pattern in Norway as in Czech Republic, although some variation is expected since the study area is situated at slightly higher latitude. In addition, April is generally a winter month in Norway (Langvatn et al. 1996) meaning that earlier than May there is still quite a lot of snow many places in the study area which prevents tick activity. Red deer in Norway start their spring migration in the beginning of May (middle migration date is 3rd of May) and migrate back to the winter areas in the start of September (Mysterud et al. 2011). In spring only 33 of the 34 transects was surveyed since the last transect was completely covered with snow. This was also the case for the very last plot of another transect that was surveyed in May. All of the 34 transects were sampled in August. To avoid differences in altitude and distance from the coast between May and August, altitudinal values and values on distance from the coast registered in August was used for May in the analyses and 0 ticks were stated in these plots. I performed most of the field work in autumn, while a field assistant performed the field work during spring.

The data on the red deer individuals is consequently not obtained in the same year as the ticks in this study was sampled. However, migration patterns of hinds do not chance between years in this area (Albon and Langvatn 1992, Langvatn and Albon 1986), and this should therefore not affect the results.

In the study area there were registered home ranges belonging to 41 red deer. Of these 18 were stationary red deer and the rest migrating. Of the home ranges belonging to migratory red deer sampled in this study, approximately half of the home ranges were winter areas and the other half were summer areas. In a few cases the transects only spanned either the winter or summer range of migratory red deer. This was the case for 7 migrating animals.

2.3 Estimation of tick abundance

Tick abundance was estimated using the cloth lure method (Vassallo et al. 2000), assumed to measure the number of questing ticks (mainly nymphs and adults), i.e., those ticks sitting on the vegetation ready to jump onto a host. Terry towels (1x0.5m) were used to collect the questing ticks since terry towels have an ideal surface for the ticks to stick on to.

Each transect consisted of 12 plots measuring about 2x10m (Figure 2). The distance between each plot was randomized between 20-50 m. In each plot the towel was swept over the ground 4 times (covering a distance of approximately 2x2 m) before the number of ticks on the towel were counted. After checking one side, it was turned around and checked on the other side too. The ticks, if present, were noted and picked off with a pair of tweezers and put on ethanol. This was repeated 5 times in each plot, thus covering a distance of approximately 10 m. The ticks were characterized in three categories; adult males, adult females or nymphs. Males and females were separated by looking on the body color. The adult females are red while the adult males are black. Nymphs are also black, but they are smaller than the adult males. In the analyses the three categories of ticks were combined and the total number of ticks collected was used in the analysis.

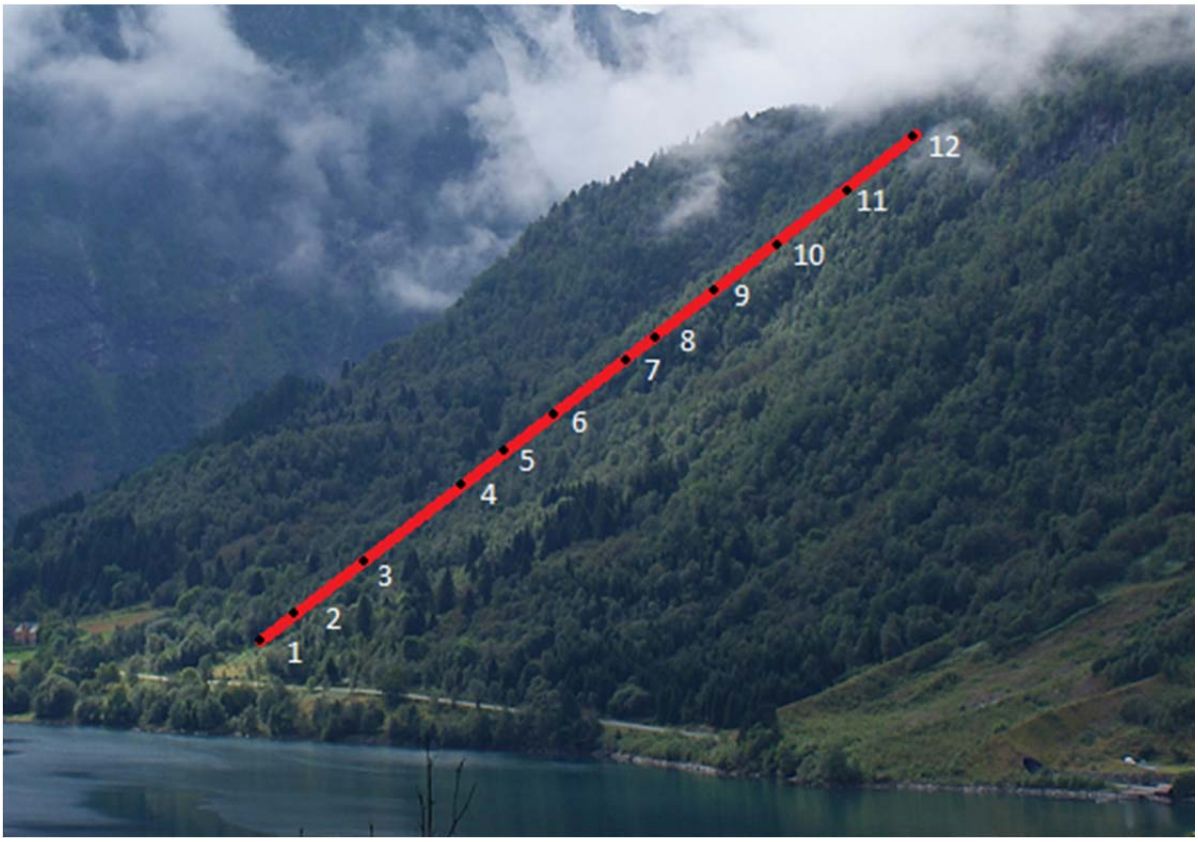


Figure 2. This figure illustrates a typical transect for surveying ticks. The black dots represent the 12 plots (2*10m) that were sampled along each transect. The photo is taken in Vetlefjorden, Sogn og Fjordane, by Nina Risnes Olsen.

I have not confirmed that all the ticks gathered belongs to the species *Ixodes ricinus*, and so might be a source of error if several species, that do not behave in a similar fashion as *I.* ricinus, is present. Still, recent studies have shown that *I. ricinus* is the dominating species in Norway (Hasle et al. 2009, Kjelland et al. 2010).

For every plot a GPS waypoint was taken to enable extraction of covariates from maps. In two cases the last waypoint of the transect is lacking. To be able to extract information for these two plots, I used a position with approximately even distance to the plot before. This will have a negligible effect on the precision of the rather coarse covariates used in this study.

2.4 Covariates

The UTM coordinates from the plots was imported into ArcGIS. On each plot position, I extracted topographic and land cover information. Altitude was extracted from the GPS and from a digital elevation model (DEM) with pixel size 100x100 m resolution. Values from all raster maps were extracted with the function Extract Values to Points in the Spatial Analyst extension of ArcGIS 9.2 (ESRI, USA). Altitudinal values extracted in ArcGIS were used in the analysis. To find distance from the coast a vector map with sea as filled polygons was used. The distance from each plot position to the closest coast line was found with the function Spatial Join in ArcGIS.

The density of red deer was calculated by using the official hunting statistics from 2009 at the municipality scale (Statistics Norway, 2009). The number of red deer harvested in 2009 was divided by the area of red deer habitat (“qualifying area”) as approved by the management authorities to yield a density estimate for each municipality (as done in Mysterud et al. 2002, 2001a). The “qualifying area” is the area of suitable red deer habitat within each municipality, constituting the basis for harvest quotas as approved by the management authorities (Mysterud et al. 2002, 2001a).

2.5 Statistical analyses

The analyses were done in two steps. In the first step the tick’s distribution in relation to different landscape factors was analysed. In the second step the relationship between tick abundance, red deer abundance and space use patterns of red deer was analysed.

All the analyses were done in R (R Development Core Team, 2010) version 2.11.1.
The main challenge with the dataset was that many plots contain zeros, which may cause ordinary Poisson models to be over-dispersed (Figure 3). Over-dispersion is common when

dealing with parasite intensity data (Rødven et al. 2009). Because of this a Poisson distribution would give a poor fit of the data. A better alternative was therefore to assume a negative binomial distribution. Initial analyses were carried out to find out which distribution was best suited for use on the data. The results showed that negative binomial distribution gave the best fit compared to zero-inflated Poisson models or ordinary Poisson models. In the process of finding the correct distribution it became evident the results were qualitatively similar regardless of the specific distribution used.

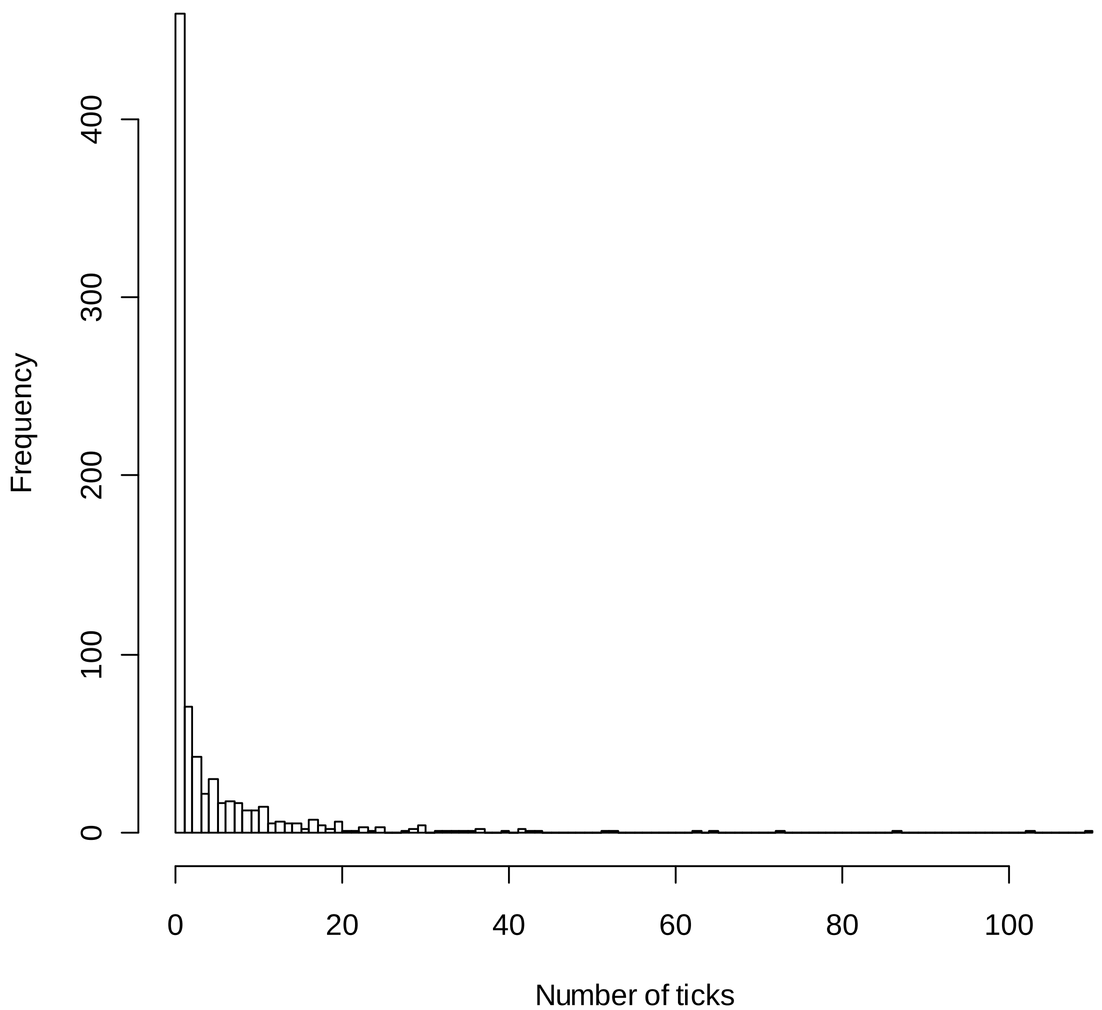


Figure 3. The histogram shows the frequency of ticks in the plots sampled. There is a large majority of plots containing zero ticks.

To check for linearity or non-linearity between response and predictor variables Generalised Additive Modelling (GAM), in the package mgcv in R was used. The initial analyses done with GAM showed an approximate linearity between tick abundance and most of the predictor variables. There were, however, indications that altitude should be modelled with a 2^{nd} order term (see appendix 1). Because of this, higher order polynomials to account for nonlinearity were included only for altitude.

Simple correlation test were also run to reveal any correlations between predictor variables. There was a weak positive correlation (r=0.471) between distance from the coast and altitude. However, a GAM-plot revealed no indication of an interaction between distance from coast and altitude (see appendix 1).

Total amount of ticks (adults and nymphs) were used as the response variable. The glm.nb function in the library MASS in R was used to determine which variables that influence tick distribution. The modeling proceeds in the same way as a typical GLM (Crawley 2007).

A model describing the amount of ticks was selected by using backwards selection (Table 1). I started with fitting the model including all predictor variables. The best model was eventually chosen based on Akaike information criterion (AIC) where the goal is to get the lowest AIC-value possible. The model with the lowest AIC value is the most parsimonious model; i.e. the best compromise between explaining most of the variation and at the same time using as few parameters as possible (Burnham and Anderson 2002). If models have the same lowest AIC value, the model with fewest parameters is chosen.

To optimize the fit of the graphs displaying tick distribution in relation to altitude and distance from coast, polynomials up to 3^{rd} order were used. Which polynomial that gave the best fit was also chosen based on AIC (see appendix 2).

3. Results

3.1 Tick distribution

In total 3491 ticks were captured, of which 2161 were caught in May and 1330 in August. Of these 3137 were nymphs, of which 1961 was collected in May and 1176 in August. Significantly fewer adults were caught; in total 178 adult females, of which 99 were collected in May and 79 in August, and 176 adult males, of which 101 were collected in May and 75 collected August, were captured.

The best model to explain the total amount of ticks is displayed in table 1. Tick distribution was influenced by several variables in addition to interactions (Table 2). As expected tick abundance was not similar throughout the year. Rather, the abundance of ticks in Sogn og Fjordane were significantly higher in May than in August. As expected in P1 there was a negative and weakly non-linear relationship between tick abundance and altitude (Table 2). In addition there was also an interaction between altitude and month. In May there were more ticks and they were generally found at a lower altitude, while in August there were fewer ticks but they were also found at higher altitudes (Figure 4).

As expected in P2 there was also a significantly negative relationship between tick abundance and distance from the coast (Table 2, Figure 5). Between distance from the coast and month, however, no interaction was found. This can be seen illustrated in figure 5. In both May and August, the shape of the curve is the same, although there is more ticks in May, especially closer to the coast (around 0 – 5000m from the coast).

Table 1. Results from model selection using AIC and a backwards selection procedure. diffAIC = AIC value minus the lowest AIC value. AICw = the probability that the model obtained is the correct model among the set of models. AICw is calculated by first making an intermediate calculation in which $e^{(\mathrm{diffAIC} \times -0.5)}$ is calculated for each diffAIC. All these values are then added together. Each of the $e^{(\mathrm{diffAIC} \times -0.5)}$ values are eventually divided on the sum of all the $e^{(\mathrm{diffAIC} \times -0.5)}$ values.

Altitude	$(\mathrm{Altitude})^2$	Distance from coast	Month	Month:altitude	Month: $(\mathrm{Altitude})^2$	Month:distance from coast	AIC	diffAIC	AICw
1	1	1	1	1	1	1	3315.3	1.1	0.365
1	1	1	1	1	1		3314.2	0	0.633
1	1	1	1	1			3326.5	12.3	0.001
1	1		1	1	1		3464.2	150	0.000

Table 2. Summary of generalized linear model with negative binomial distribution analyzing the influence of the explanatory variables on the abundance of ticks. The baseline (intercept) here is the month August.

	Estimate	Std. Error	Z	p
-Intercept	1.955	0.155	12.594	< 0.001
Altitude	-1.302×10^{-03}	1.115×10^{-03}	-1.169	0.243
$(\mathrm{altitude})^2$	-2.881×10^{-07}	1.303×10^{-06}	0.221	0.825
Distance from coast	-1.577×10^{-04}	1.316×10^{-05}	-11.986	< 0.001
Month (May vs. August)	0.218	0.232	0.939	0.348
Altitude:month(May)	4.738×10^{-03}	2.011×10^{-03}	2.356	0.018
$(\mathrm{altitude})^2$:month(May)	-1.180×10^{-05}	3.387×10^{-06}	-3.483	<0.001

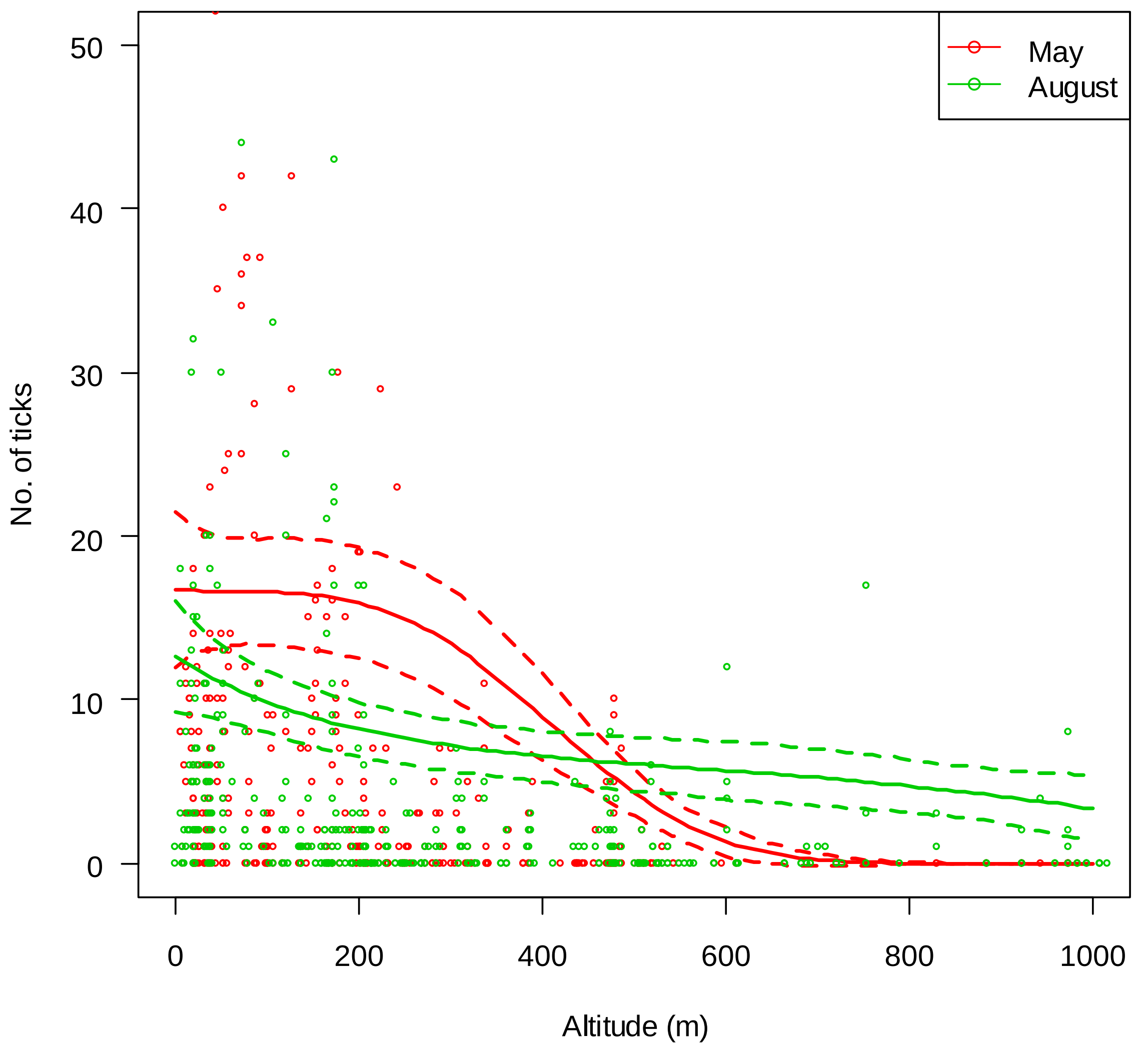


Figure 4. Abundance of ticks in relation to altitude and month in Sogn og Fjordane, Norway. The dots indicate values sampled in the field. The lines are made by using a third order polynomial to optimize the fit of the lines to the points (see appendix 2). Dotted lines represent 95% confidence limits. In May (red) there are more ticks than in August (green), but ticks can be found at higher altitudes in August than in May. To make it better for the reader to see the trends in the graph some outliers have been left out and the y-axis has been cropped. The complete graph with outliers, in addition to AIC values, can be found in appendix 2.

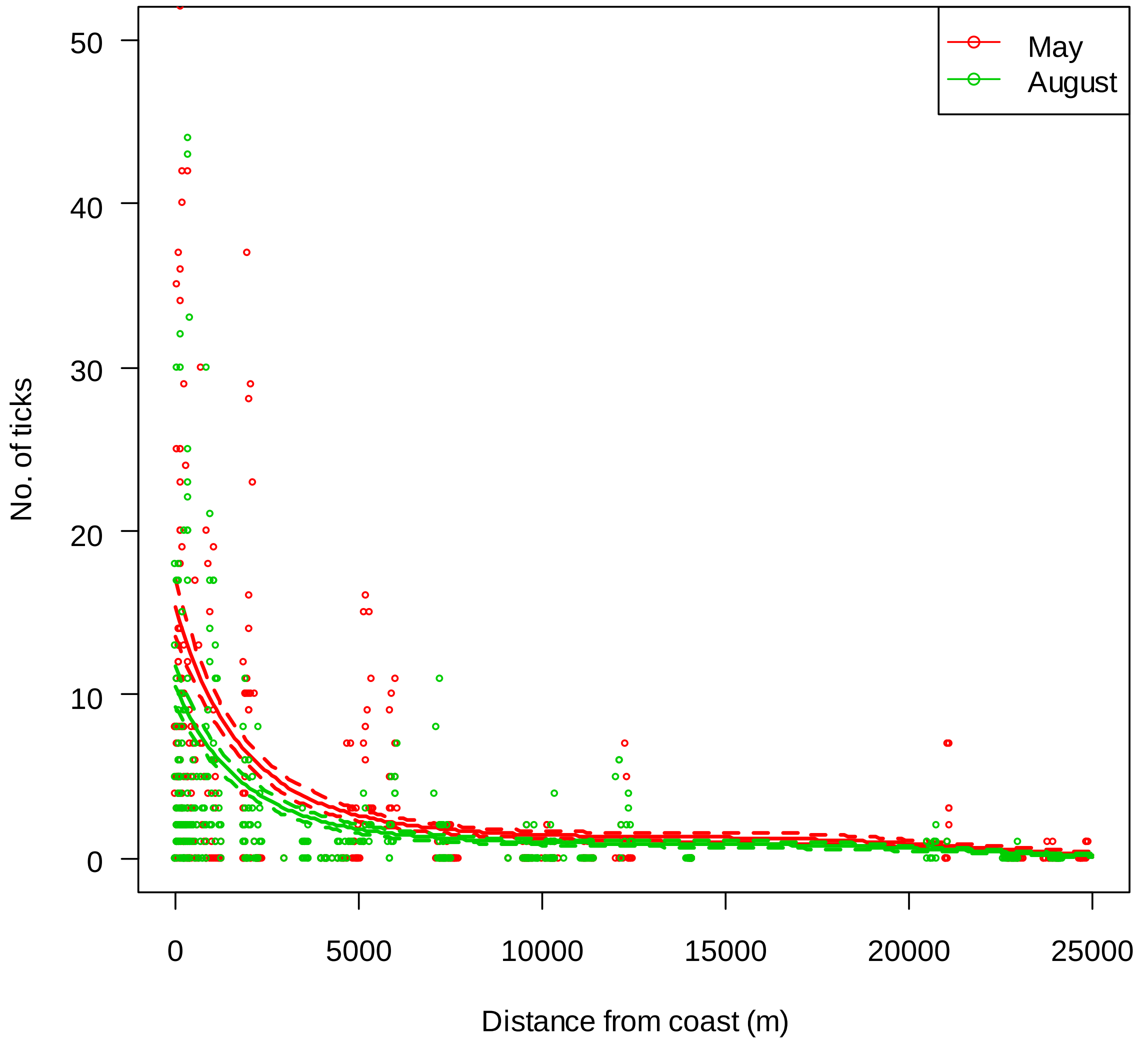


Figure 5. Abundance of ticks in relation to distance from coast and month in Sogn og Fjordane, Norway. The dots indicate values sampled in the field. The lines are made by using a third polynomial to optimize the fit of the lines to the points (see appendix 2). Dotted lines represent 95% confidence limits. There is no interaction between distance from coast and month. The lines are divided in May and August to illustrate that there are more ticks in May than August. Some outliers have been left out and the y-axis cropped to make it better for the reader to see the trends in the graph. The complete graph with outliers, in addition to AIC values, can be found in appendix 2.

3.2 Ticks distribution and migration pattern of red deer

In this part of the analysis the data set was arranged so that were more than one red deer were present in a transect, the transect was amplified for each of the individual deer. A total of 576 of the plots sampled along the 34 transects in May and August was situated in home ranges of stationary red deer, while 984 of the plots was situated in home ranges of migrating red deer. Of these 480 plots was situated in summer areas and 504 was situated in winter areas.

Table 3. The influence of home range type and density of red deer on the total amount of ticks in the landscape. The baseline (intercept) is stationary red deer home range.

	Estimate	Std. Error	Z	p
(Intercept)	3.4094	0.3177	10.732	< 0.001
Migratory summer	-1.1674	0.1150	-10.155	< 0.001
Migratory winter	-0.4427	0.1100	-4.025	<0.001
Red deer density	-0.7995	0.1450	-5.514	<0.001

Surprisingly, there seems to be a negative relationship between density of red deer and tick abundance (Table 3). This means that prediction P3, that there is a positive relationship between deer density and tick abundance is not supported.

As expected from P4 the home range belonging to stationary red deer contains the largest amount of ticks in Sogn og Fjordane (Table 3, Figure 6, Figure 7). There were significantly fewer ticks in winter and summer areas compared to stationary home ranges. The smallest quantities of ticks were found in summer areas which are normally situated at the highest altitudes and furthest away from the coast. The amount of ticks in the summer areas of migratory deer were actually halved compared to the amount found in home ranges of stationary red deer. In the winter ranges of migratory deer, which is normally situated at altitudes and distance from the coast somewhere in between that of stationary and summer ranges, the amount of ticks were half way in between what was found in stationary and summer ranges. This is illustrated in figure 6 and 7 which show the mean number of ticks in red deer home ranges in relation to altitude and distance from the coast respectively. In both figures one can see that there were generally more ticks in May than in August in all red deer home ranges and in fact, the amount of ticks was almost halved for all of the home ranges in August compared to May. The mean value of ticks in the home range types in figure 6 coincide with the tick distribution obtained in figure 4 with more ticks in areas at lower altitudes. In the same way the values in figure 7 coincide with the tick distribution in figure 5.

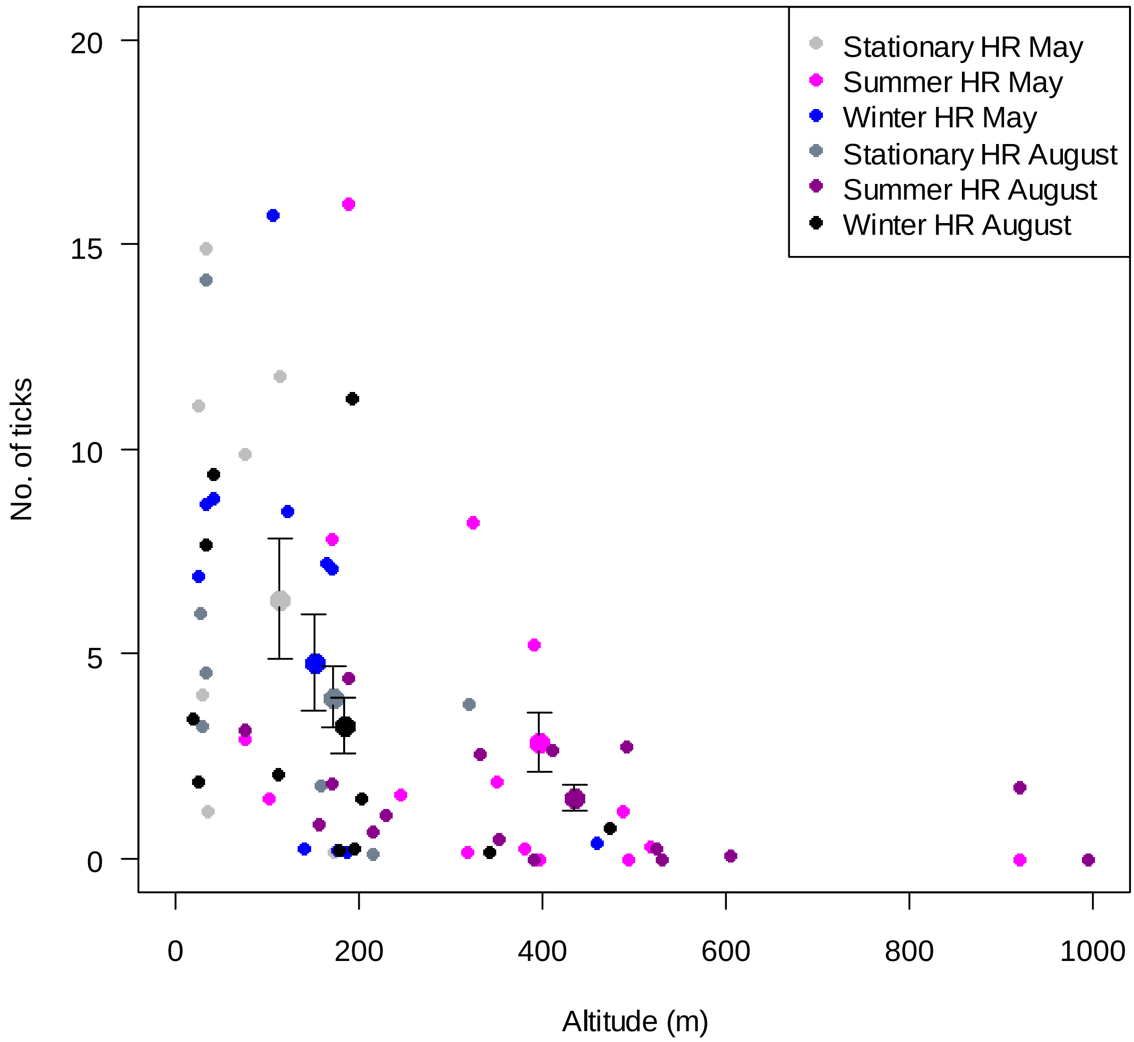


Figure 6. Number of ticks in red deer home ranges in relation to altitude and month in Sogn og Fjordane, Norway. Small dots represent mean number of ticks and mean altitude for individual red deer by home range type. The large circles give the mean value for the three home range types; stationary (grey), summer (magenta) and winter (blue). The dark colors gives the August values while the lighter colors indicate values obtained in May. The 95% confidence intervals are indicated by brackets and show very little variation in the number of ticks for each of the mean values. Stationary ranges are situated at lowest altitudes and have the largest amounts of ticks. In the migratory ranges, winter ranges is situated at higher altitudes and have a smaller amount of ticks. The summer ranges have the smallest amount of ticks and are situated at the highest altitudes. There are generally more ticks in May than in August. There is some discrepancy in the mean altitude for the home range types between May and August. This is most likely due to margin of error in the GPS and to the fact that two different persons did the fieldwork in May vs. August.

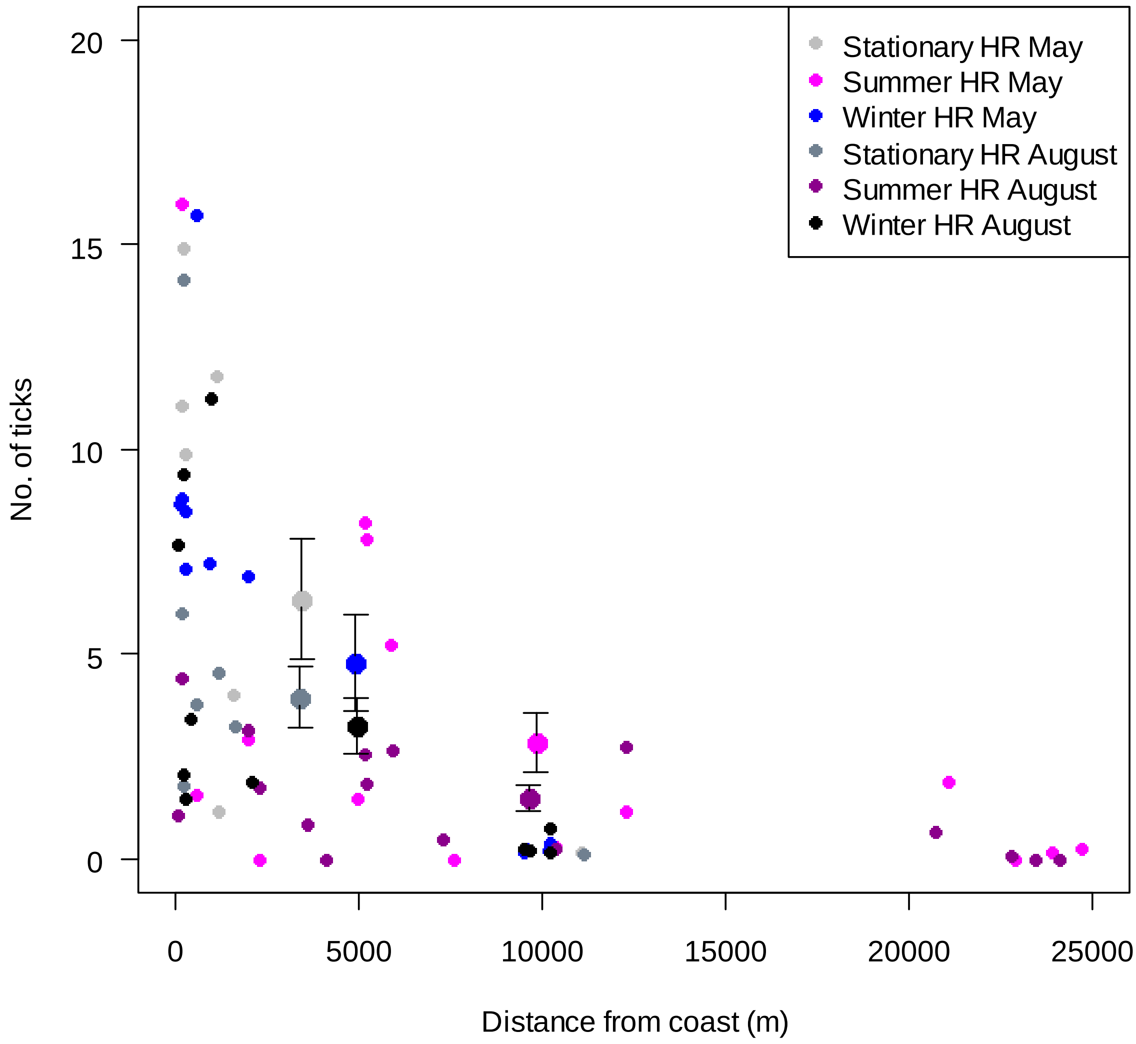


Figure 7. Number of ticks in red deer home ranges in relation to distance from coast and month in Sogn og Fjordane, Norway. Small dots represent mean number of ticks and mean distance from the coast for individual red deer by home range type. The large circles give the mean value for the three home range types; stationary (grey), summer (magenta) and winter (blue). The dark colors gives the August values while the lighter colors indicate values obtained in May. The 95% confidence intervals are indicated by brackets and show very little variation in the number of ticks in each of the mean values. Stationary ranges are situated closest to the coast and have the largest amounts of ticks. The winter ranges of migratory red deer are situated further inland and have a smaller amount of ticks. The summer ranges have the smallest amount of ticks and are situated farthest away from the coast. There are generally more ticks in May than in August.

4. Discussion

The influence of landscape level variation on tick abundance is important to study due to the large influence of ticks on both wild and domesticated animals as well as on humans. The large tick burdens may restrain people in their use of the landscape for recreational purposes. In addition, the infection and illness that can be caused by pathogens in ticks can be severe and long lasting. Heavy tick loads on animals can itself be problematic in terms of blood loss and possible also infection at the bite site. In regards to red deer in Norway the impact of ticks on the space use patterns of red deer has not been much studied and is of big interest due to the importance of red deer as a game species.

4.1 Tick abundance

The winter 2008/2009 in Norway as a whole was warm with a mean temperature 1.3°C above normal and a precipitation just below normal (The Norwegian Meteorological Institute 2010, 2009a). Winter climate is important for the over winter survival of ticks (Neelakanta et al. 2010, Lindgren et al. 2000). Temperatures below freezing without the protection of snow is thought to be especially devastating for ticks, although studies on *I. scapularis* indicate that engorged ticks (Ginsberg et al. 2004, Lindsay et al. 1995) and ticks infected by *Anaplasma phagocytophilum* (Neelakanta et al. 2010) may have a better chance of surviving in the cold. Snow cover however, insulates and sees that the temperature close to the ground rarely falls below 0°C and thereby increasing tick survival (Materna et al. 2008, Lindsay et al. 1995). From the climatic records it seems that the winter 2008/2009 in Norway was more or less normal. In May 2009 the mean daily maximum air temperature in Førde municipality (recorded at Førde airport 61°23′28″N 5°45′25″E), which is situated more or less in the middle of the study area, was 11.8°C. The mean temperature for the whole month here was 8°C, which is 0.3°C warmer than normal (The Norwegian Meteorological Institute 2009c). In August 2009 the mean daily maximum air temperature at Førde airport at was 16.2°C. The mean temperature for the whole month here was 12.8°C, which is 0.9°C warmer than normal (The Norwegian Meteorological Institute 2009b). In Slovenia Knap et al. (2009) found that tick nymphs and adults of *I.* ricinus became active as soon as daily maximum temperature exceeded 7°C and the snow had melted. Consequently, when the fieldwork in this study was started in May the daily maximum temperature had exceeded 7°C and ticks had most likely become active in all areas except in areas where there were still snow covering the ground or were it still was very wet after the snow had melted. In Slovenia start of tick season happened typically in March, but in some places as early as February. In Norway it is likely that tick activity is delayed because of lower temperatures and longer snow cover since Norway is situated further north. The mean maximum temperature in April was 6.9°C (The Norwegian Meteorological Institute 2009d), thus just below the assumed threshold.

The abundance and/or activity of ticks change throughout the year in Sogn og Fjordane. In May there was a higher abundance and/or activity of ticks in the landscape than in August. A limitation of the cloth lure method, however, is that it is difficult to distinguish between increased abundance and increased activity in the area sampled. I have indeed no firm basis for distinguish whether there were more ticks in May because there were more ticks in the vegetation, or whether it was because of a higher activity in ticks in May. The cloth lure method is not nor suitable for collecting larvae because they are situated more deeply in the vegetation to avoid low humidity (Ruiz-Fons and Gilbert 2010, Knap et al. 2009). Larvae were therefore not included in the study. It was neither distinguished between nymphs and adults in the analysis, although the nymphs clearly dominated in both months. The same trend has also been found in other studies (Gilbert 2010, Nazzi et al. 2010, Knap et al. 2009, Schwarz et al. 2009). This may be an indication that few nymphs survive to the adult stage, or that adults have a lower survival rate. Lindsay et al. (1995) found that unfed adult *I. scapularis* ticks had a lower over winter survival rate than unfed nymphs.

The meteorological data gives support to the assumption that ticks in Sogn og Fjordane will most likely be most active in May as soon as the local conditions meet the requirements for tick activity. The faster the ticks become active the faster they can find a host. It is crucial for ticks to find a host before the conditions becomes too dry. Several studies report the same trend, that tick activity peaks in spring and gradually decline throughout summer and fall (Nazzi et al. 2010, Knap et al. 2009, Schwarz et al. 2009). A likely reason for this is that a portion of the ticks that hatched or became active after the winter diapause in spring have found a host or is likely to have died before August. Another likely explanation is that ticks become less active as summer progress and the landscape dries as a strategy to avoid desiccation (Knap et al. 2009, Schwarz et al. 2009). The west coast of Norway however, normally experiences a wet climate all year round, especially in coastal areas, and 2009 does not seem to have been any deviation from the norm (The Norwegian Meteorological Institute 2010). On the other side, in late summer and fall, studies in Germany (Schwarz et al. 2009) and Slovenia (Knap et al. 2009) have shown that ticks that found a host early in spring may have been able to lay eggs, that hatch in fall, or have been able to make the transition to the next life stage in fall. Tick activity consequently shows a bimodal seasonal pattern in some areas. Such a bimodal pattern is also seen in Italy (Nazzi et al. 2010). If this is the case also in Norway, the tick activity measured in August in this study might be a minor peak in tick activity and not just a part of a gradual decline in activity as summer progress. Whether or not this is the case in Sogn og Fjordane I have no basis for saying, and would be interesting to investigate further. It might be the case that the summer in Norway is too short to enable this.

A negative and slightly non-linear relationship between tick abundance and altitude was found in Sogn og Fjordane, confirming what several other studies have found in other countries (Gilbert 2010, Materna et al. 2008, Rand et al. 2003). The tick distribution also changed along the altitudinal gradient throughout the year in the study area. In May there was a higher tick abundance and the tick distribution reached moderate altitudes (600 m above sea) as opposed to August when the abundance was lower but the distribution reached higher altitudes (1000 m above sea) as well. In May there is still some snow and very wet several places higher up in the mountains in Sogn og Fjordane, which makes it less suitable for ticks here in this period. Also, at higher altitudes there might be high humidity over a longer period because of a later snow melt, but because the temperature also is lower since the temperature falls 0.6°C per 100 m elevation in Norway, it is most likely not very well suited for ticks, at least not until later in the year. In August, however, the conditions have become suitable for egg hatching and nymph activity also at higher altitudes. This is a likely explanation for why the upper distribution of ticks shifted to higher altitudes in August when this region is drier and warmer in Norway.

In the same way as with altitude, there were a negative relationship between tick abundance and distance from the coast. The tick abundance was also higher in May than in August along this gradient, but there was no interaction with month. The higher humidity associated with a more marine climate might enhance tick survival in this environment and may be the explanation for the observed relationship. This is also proposed for *I. scapularis* ticks in North America (Rand et al. 2003). Higher temperatures associated with the coastal areas in Norway as a consequence of the Gulf Stream is also a likely contributing factor to a higher tick abundance closer to the coast. It is the ticks' vulnerability to desiccation that makes high humidity so important. To a large extent a tick may control dehydration by taking advantage of microclimate conditions including moving closer to the ground where the humidity is higher. Still it may be advantageous to be located in an area that generally has high humidity.

It is, however, important to emphasize that the trend seen is thus not a direct effect of altitude and distance from the coast; instead it is likely a result of variation in temperature and humidity induced by the distance from the coast and altitude. There was a weak correlation between altitude and distance from the coast. However, initial analysis showed that the correlation was not big enough to influence the results.

4.2 Tick abundance and red deer density

One would generally assume a positive relationship between parasite and host density (Stanko et al. 2002). It was therefore surprising to find that deer density was negatively related to tick abundance in Sogn og Fjordane. Especially since recent studies have found a clear positive relationship between tick and deer abundance (e.g. Gilbert 2010, Ruiz-Fons and Gilbert 2010). Also in North America Rand et al. (2003) found a positive, although weak, relationship between *I. scapularis* and white-tailed deer, *Odocoileus virginianus*, density. Red deer density was in this study measured at a coarse municipality scale. It might be the case that deer density closer to the individuals' home ranges, and thus closer to transects sampled, is more important. It could indeed be that a local measure of red deer density would have given another result, and that looking at red deer density at the municipality level does not reflect the actual density in transects. Other studies (e.g. Gilbert 2010, Ruiz-Fons and Gilbert 2010) have used faecal pellet group counts as a measure of deer density and should be considered in any future studies.

On the other side Ostfeld et al. (2006) concluded that deer abundance did not affect subsequent *Ixodes scapularis* nymph abundance. This observation supports the finding of Van Buskirk and Ostfeld (1995) that, once deer abundance exceeds a low threshold value, further increases in deer density will have little if any effect on tick densities. Even though these studies deal with another tick species, it is likely that the same applies for *I. ricinus* and that this may be the case in Sogn og Fjordane. Red deer abundance is generally very high in this county, and local variability in red deer density might therefore not influence tick abundance further. It is also possible that hosts other than red deer are more important in influencing tick abundance in Sogn og Fjordane. In addition, hosts for *I. ricinus* larvae such as rodents might be more important in controlling the abundance of nymphs and adult ticks than the nymphs and adult ticks themselves. Van Buskirk and Ostfeld (1995) emphasize that hosts for nymphs and especially adult ticks are often very big and can sustain a large amount of ticks compared to small mammals that are hosts for larvae. Small mammals may thus be more important in controlling the tick population than larger mammals that acts as hosts for nymphs and adults.

Ruiz-Fons and Gilbert (2010) emphasize the need to take into account local variables such as alternative hosts and ground vegetation when studying questing tick abundance and may be something that future studies should take into account. If rodents are an important controlling factor of the tick population, then tick abundance might also be related to the cycle of rodents. In addition the food supply for small mammal hosts may also indirectly influence tick abundance by controlling the host populations (Ostfeld et al. 2006).

4.3 Red deer migration pattern

Cervids are important potential hosts affecting the spread of ticks and tick-borne diseases (Buskirk and Ostfeld 1995, Ostfeld et al. 2006, Ruiz-Fons and Gilbert 2010, Rosef et al. 2009, LoGiudice et al. 2008). To my knowledge no previous study has focused on the potential influence of ticks on migration pattern of large herbivores such as red deer. In Norway red deer show partial migration, something which is common in ungulates living in highly seasonal environments (Mysterud et al. 2011). Migration routes are traditional, and differences in migratory behavior appear to be determined by the migratory behavior of the maternal ancestor (Albon and Langvatn 1992). Much is known about the main triggers for migration in red deer. It is unlikely that tick abundance is the main driver of migration, which is likely linked to plant phenology, as deer migrate also in areas without ticks (Hebblewhite et al. 2008). Previous studies have shown that red deer gain from a prolonged access to newly emerged forage along an altitudinal gradient as they migrate to higher altitudes during spring migration (Mysterud et al. 2001b). Consequently, red deer may benefit by staying in an area with variable topography (Mysterud et al. 2001b). The social fencing hypothesis and the competition avoidance hypothesis have also been suggested as additional explanations to plant phenology for why red deer migrate to summer areas (Mysterud et al. 2011). The reason for spring migration is, however, still a bit uncertain. Migration in fall to winter ranges at lower altitudes, on the other side, is most likely forced by snow depth (Mysterud et al. 2011). In this study the placement of red deer home ranges along altitudinal and coast-inland gradients coincides with tick abundance. The home ranges belonging to stationary deer was situated at lower altitudes and closest to the coast compared to migratory areas. It was also in these areas the largest abundances of ticks were found both in May and August. Further inland and at higher altitudes the tick abundance decreases. The decrease coincided well with the location of winter and summer red deer home ranges. Fewest ticks were found at the highest elevations in areas were summer ranges of migratory deer was located. Winter areas of migratory deer was positioned at an altitude and distance from coast in between, relative to ranges belonging to stationary deer and summer ranges belonging to migratory deer. The amount of ticks found in winter ranges lay in between the amounts found in stationary and summer ranges. Still, there was some natural overlap between the home range types when looking on the values for each of the individual red deer (the small dots in figure 6 and 7). For example some of the summer ranges were situated at lower altitudes and thus had a higher amount of ticks in the landscape.

I assume that an increase in ticks captured with the cloth lure method leads to the red deer in the area having an increase in tick load. The results in this thesis thus give support to the hypothesis that deer that migrate further away from the coast and to higher altitudes in the summer benefit by avoiding areas likely to yield a heavy tick load. Even though tick abundance is not the main reason for red deer migration, this study at least indicates a further benefit of migration. It is valid to assume that very heavy tick loads will be a disadvantage to red deer. Both the direct effects of removing blood and indirect by disease transmission may play a role. One of the limitations in this study is that I do not know much about the red deer in this study with regards to fitness and tick load on the animals. It should therefore be investigated whether stationary deer actually have a higher tick load on them, or if they manage to compensate in some way to avoid heavy tick loads. Matuschka et al. (1993) argue that ungulate hosts may have an internal property such as a physiologic or immunological peculiarity that regulates tick load because they failed to find any apparent ecologic or physical correlation between the size of the host and tick load in their study.

It has been demonstrated that body weight of red deer increases with latitude and distance from the coast (Langvatn and Albon 1986). This variation in body weight also causes variation in ovulation rates in hinds (Langvatn et al. 1996).Langvatn and Albon (1986) argue that the reason for this increase in body weight is plant phenology. Plants tend to have an increased digestibility from coast to inland. In addition, heterogeneity of snow melt at higher altitudes and latitudes gives animals a longer availability of new plant growth. Red deer living further north and further inland consequently have access to higher quality diets over a relatively longer period of time during summer. In this study though, an additional reason for this pattern might be that deer experiences heavier tick loads at lower altitudes and closer to the coast. Heavy tick loads may induce stress in deer and prevent them from reaching the same body weight as deer living in areas with less tick burdens. A study on moose, *Alces alces*, by Glines and Samuel (1989) in North America showed that infestation by winter tick, *Dermacentor albipictus*, led to hair loss, weight loss and anemia in addition to other changes in blood composition. It is not unlikely that some of the same effects can be caused by *I. ricinus* ticks in red deer giving more support to the hypothesis that migrating deer gain an advantage by avoiding areas likely to yield a heavy tick load. I have however, not succeeded in finding any studies that support hair loss as a consequence of tick infestation in red deer. In addition, physiological stress and energetic demands of migration can alter the outcome of infection as migration may affect the immune system and making the animals more prone to parasite attack and infection (Altizer et al. 2011), and may thus be an additional explanation for why not all deer migrate.

I can however, not rule out the possibility that the ecology of tick and red deer simply correlate and do not actually have anything to do with each other. Still, based on the results of this and other studies I find this hard to believe as red deer clearly is an important host for *Ixodes* ticks. On the basis of this study future studies can investigate the relationship between ticks and red deer in Norway and thereby determine how important tick abundance is for the migration patterns of red deer and how tick loads affect deer physically.

4.4 Management implications

In this study ticks were found at altitudes as high as 1000 m above sea and ticks can most likely be found at even higher altitudes in this area. Samples were not taken at higher altitudes in this study. This study can make the basis for a surveillance study of the distribution and abundance of ticks in Sogn og Fjordane. A long term study in this area would allow trends in tick abundance and distribution to be revealed, and would be important for both management and research. With more knowledge it could be possible to predict the tick load in the landscape in subsequent years. If we can better understand how the distribution of ticks react to different variables it can be of good use to the public and can be taken into consideration in for example the use of the landscape for recreational purposes. Increased knowledge of ticks may also possibly be used in wildlife management in terms of mange deer to reduce the risk of tick-borne diseases or possible to give advice on where and when it is most proper for farm animals to graze in terms of avoiding areas likely to yield heavy tick loads. It may also be important for Health Institutes in the way that they can give even better information to the public about ticks and what can be done to prevent encounters. A study by Nazzi et al. (2010) also suggests that the density of ticks in an area can be used to predict the risk for borreliosis in that area. In this study I focused on the total amount of ticks collected. Future studies could also look more at what life stages are present in different areas at which time and whether different variables are important for the different life stages.

5. Conclusion

In conclusion, tick abundance was influenced by several variables in Sogn og Fjordane, Norway. A higher tick abundance and/or activity were registered in May than in August. I suggest that a possible explanation for the observed pattern is that ticks that became active in May might have found a host or is likely to have died before August. Another possibility is that fewer ticks were sampled in August because there was a lower tick activity in the landscape as a result of a drier environment in fall. The observed pattern may be a result of a combination of these explanations that was not possible to distinguish between as the cloth lure method is not suited to distinguish between activity and abundance. Lower temperatures and lower humidity further inland and at higher altitudes is proposed as an explanation for the negative relationship found between tick abundance and altitude and distance from the coast. Since it takes longer for the conditions to become suitable for tick activity at higher altitudes in spring, tick abundance along the altitudinal gradient was different in spring and fall. Surprisingly, a negative relationship between red deer density and tick abundance was found. A likely explanation for this is that the density of red deer already is so high in Sogn og Fjordane that local variation in deer density will not have an additional effect on tick density. It may also be the case that other hosts, such as small mammals, are more important in controlling the tick population than red deer. Finally, summer home ranges belonging to migratory red deer had the lowest amounts of ticks. The largest amounts of ticks were collected in home ranges belonging to stationary deer. This means that red deer migrating further away from the coast and to higher altitudes in the summer receive an additional benefit in terms of avoiding areas likely to yield heavy tick loads. This study thus gives a possible additional explanation for why red deer migrate. Although more detailed studies are needed on these topics this study contributes with more knowledge on tick abundance in Norway and gives a new and exciting view on red deer migration.

References

Abrahamsen, J., Jacobsen, N.K., Kalliola, R., Dahl, E., Wilborg, L. And Påhlsson, L. 1977. Naturgeografisk region-inndeling av Norden. *Nordiske Utredn Ser B* **34:** 1-137 [In Norwegian]

Albon, D. and Langvatn, R. 1992. Plant phenology and the benefits of migration in a temperate ungulate. *Oikos* **65:**502-513

Altizer, S., Bartel, R., Han, B.A. 2011. Animal migration and infectious disease risk. *Sience* **331:** 296-302

Burnham, K.P. and Anderson, D.R. *Model selection and multimodel inference. A practical information-theoretic approach.* New York: Springer, 2002. 488 pages.

Colman, J.E., Pedersen, C., Hjermann, D.Ø., Holand, Ø., Moe, S.R. and Reimers, E. 2003. Do wild reindeer exhibit grazing compensation during insect harassment? *The Journal of Wildlife Management.* **67:** 11-19

Crawley, M. J.: *The R book*. John Wiley & Sons, Ltd. 2007. 942 pages

Fauchald, P., Rødven, R., Bårdsen, BJ., Langeland, K., Tveraa, T., Yoccoz, N.G. and Ims, R.A. 2007. Escaping parasitism in the selfish herd: age, size and density-dependent warble fly infestation in reindeer. *Oikos* **116:** 491-499

Folstad, I., Nilssen, A.C., Halvorsen, O. and Andersen, J. 1991. Parasite avoidance – the cause of post-calving migrations in Rangifer. *Canadian Journal of Zoology-Revue Canadienne De Zoologie* **69:** 2423–2429

Gilbert, L. 2010. Altitudinal patterns of tick and host abundance: a potential role for climate change in regulating tick-borne diseases? *Oecologia* **162:** 217-225

Ginsberg, H.S., Zhioua, E., Mitra, S., Fischer, J., Buckley, P.A., Verret, F., Underwood, H.B. and Buckley, F.G. 2004. Woodland type and spatial distribution of nymphal *Ixodes scapularis* (Acari: Ixodidae). *Environmental Entomology* **33:** 1266-1273

Glines, M.V. and Samuel, W.M. 1989. Effect of *Dermacentor albipictus* (Acari: Ixodidae) on blood composition, weight gain and hair coat of moose, *Alces alces. Experimental & Applied Acarology* **6:** 197-213

Gordon, I.J., Hester, A.J. and Festa-Bianchet, M. 2004. The management of wild large herbivores to meet economic, conservation and environmental objectives. *Journal of Applied Ecology* **41:** 1021-1031

Hagemoen, R.I.M. and Reimers, E. 2002. Reindeer summer activity pattern in relation to weather and insect harassment. *Journal of Animal Ecology* **71:** 883-892

Hasle, G., Bjune, G., Edvardsen, E., Jakobsen, C., Linnehol, B., Røer, J.E., Mehl, R., Røed, K.H., Pedersen, J. and Leinaas, H.P. 2009. Transport of ticks by migratory passerine birds to Norway. *Journal of Parasitology* **95:** 1342-1351

Hebblewhite, M., Merrill, E. and McDermid, G. 2008. A multi-scale test of the forage maturation hypothesis in a partially migratory ungulate population. *Ecological Monographs* **78:** 141-166

Helle, T., Aspi, J., Lempa, K. and Taskinen, E. 1992. Strategies to avoid biting flies by reindeer-field experiments with silhouette traps. *Annales Zoologici Fennici* **29:** 69-74

Knap, N., Durmiši, E., Saksida, A., Korva, M. and Petrovec, M. 2009. Influence of climatic factors on dynamics of questing *Ixodes ricinus* ticks in Slovenia. *Veterinary Parasitology* **164:** 275-281

Kjelland, V., Stuen, S., Skarpaas, T. and Slettan, A. 2010. *Borrelia burgdorferi* sensu lato in *Ixodes ricinus* ticks collected from migratory birds in Southern Norway. *Acta Veterinaria Scandinavica* **52:** 59

Langvatn, R., Mysterud, A., Stenseth, N.C., and Yoccoz, N.G. 2004. Timing and synchrony of ovulation in red deer constrained by short northern summers. *American Naturalist* **163:** 763-772

Langvatn, R., Albon, S.D., Burkey, T. and Clutton-Brock, T.H. 1996 Climate, plant phenology and variation in age of first reproduction in a temperate herbivore. *Journal of Animal Ecology* **65:** 653-670

Langvatn, R. and Albon, S.D. 1986. Geographic clines in body weight of Norwegian red deer: a novel explanation of Bergmann's rule? *Holarctic Ecology* **9:** 285-293

Lindgren, E., Tälleklint, L. and Polfeldt, T. 2000. Impact of climatic change on the northern latitude limit and population density of the disease-transmitting European tick *Ixodes ricinus. Environmental Health Perspectives **108:** 119-123*

Lindsay, L.R., Barker, I.K., Surgeoner, G.A., McEwen, S. A., Gillespie, T.J. and Robinson, J.T. 1995. Survival and development of *Ixodes scapularis* (Acari: Ixodidae) under various climatic conditions in Ontario, Canada. *Entomological Society of America* **32:** 143-152

LoGiudice, K., Duerr, S.T.K., Newhouse, M.J., Schmidt, K.A., Killilea, M.E. and Ostfeld, R.S. 2008. Impact of host community composition on Lyme disease risk. *Ecological Society of America* **89:** 2841-2849

Materna, J., Milan, D., Metelka, L. and Harčarik, J. 2008. The vertical distribution, density and the development of the tick *Ixodes ricinus* in mountain areas influenced by climate changes (The Krkonoše Mts., Czech Republic). *International Journal of Medical Microbiology* **298:** 25-37

Matuschka, FR., Heiler, M., Eiffert, H., Fischer, P., Lotter, H. and Spielman, A. 1993. Diversionary role of hoofed game in the transmission of Lyme disease spirochetes. *The American Society of Tropical Medicine and Hygiene* **48:** 693-699

McShea, W.J. and Underwood, H.B. *The science of overabundance. Deer ecology and population management.* Washington, D.C.: Smithsonian Institution Press. 1997. 402 pages.

Milner, J., Bonenfant, C., Mysterud, A., Gaillard, J.-M., Csányi, S., and Stenseth, N.C. 2006. Temporal and spatial development of red deer harvesting in Europe - biological and cultural factors. *Journal of Applied Ecology* **43:** 721-734.

Mysterud, A., Loe, L.E., Zimmermann, B., Bischof, R., Veiberg, V. and Meistingset, E. 2011. Partial migration in expanding red deer populations at northern latitudes – a role for density dependence? *Oikos in press*

Mysterud, A., Yoccoz, N.G., Stenseth, N.C., and Langvatn, R. 2001a. Effects of age, sex, and density on body weight of Norwegian red deer: evidence of density-dependent senescence. *Proceedings of the Royal Society of London, Series B* **268:** 911-919

Mysterud, A., Langvatn, R., Yoccoz, N.G. and Stenseth, N.C. 2001b. Plant phenology, migration and geographical variation in body weight of a large herbivore: the effect of a variable topography. *Journal of Animal Ecology* **70:** 915-923

Mysterud, A., Stenseth, N.C., Yoccoz, N.G., Langvatn, R. and Steinheim, G. 2001c. Nonlinear effects of large-scale climatic variability on wild and domestic herbivores. *Nature* **410:** 1096-1099

Mysterud, A., Yoccoz, N.G., Stenseth, N.C. and Langvatn, R. 2000. Relationships between sex ratio, climate and density in red deer: the importance of spatial scale. *Journal of Animal Ecology* **69:** 959-974

Nazzi, F., Martinelli, E., Del Fabro, S., Bernardinelli, I., Milani, N., Iob, A., Pischiutti, P., Campello, C. and D'Agaro, P. 2010. Tick and Lyme borreliosis in an alpine are in northeast Italy. *Medical and Veterinary Entemology* **24:** 220-226

Neelakanta, G., Sultana, H., Fish, D., Anderson, J.F. and Fikrig, E. 2010. *Anaplasma phagocytophilum* induces *Ixodes scapularis* ticks to express an antifreeze glycoprotein gene that enhances their survival in the cold. *The Journal of Clinical Investigation* **120:** 3179-3190

Ostfeld, R.S., Canham, C.D., Oggenfuss, K., Winchcombe, R.J. and Kessing, F. 2006. Climate, deer, rodents, and acorns as determinants of variation in lyme-disease risk. *PLoS Biology* **4:** 1058-1068

Rand, P.W., Lubelczyk, C., Lavigne, R.G., Elias, S., Holman, M.S., Lacombe, E.H. and Smith, R.P. Jr. 2003. Deer density and the abundance of *Ixodes scapularis* (Acari: Ixodidae). *Journal of Medical Entomology* **40:** 179-184

R Development Core Team (2010) *R: A language and environment for statistical computing*, [2.11.1] edn. Vienna, Austria, R Foundation for Statistical Computing.

Rosef, O., Paulauskas, A. and Radzijevskaja J. 2009. Prevalence of *Borrelia burgdorferi* sensu lato and *Anaplasma phagocytophilum* in questing *Ixodes ricinus* ticks in relation to the density of wild cervids. *Acta Veterinaria Scandinavica* **51:** 47

Rosef, O., Radzijevskaja, J., Paulauskas, A. and Haslekås, C. 2008. The prevalence of *Anaplasma phagocytophilum* in host-seeking *Ixodes ricinus* ticks in Norway. *Clinical Microbiology and Infection* **15:** 43-45

Ruiz-Fons, F. and Gilbert, L. 2010. The role of deer as vehicles to move ticks, Ixodes ricinus, between contrasting habitats. *International Journal of Parasitology* **40:** 1013-1020

Rødven R., Männikkö I., Ims R. A., Yoccoz N. G. and Folstad I. 2009. Parasite intensity and fur coloration in red deer calves – contrasting artificial and natural selection. *Journal of Animal Ecology* **78:** 600-607

Scharlemann, J. P. W., Johnson, P. J., Smith, A. A., Macdonald, D. W. and Randolph, S. E. 2008. Trends in ixodid tick abundance and distribution in Great Britain. *Medical and Veterinary Entemology* **22:** 238-247

Schwarz, A., Maier, W.A., Kistemann, T. and Kampen, H. 2009. Analysis of the distribution of the tick *Ixodes ricinus* L. (Acari: ixodidae) in a nature reserve of western Germany using Geographic Information Systems. *International Journal of Hygiene and Environmental Health* **212:** 87-96

Stanko,M., Miklisová, D., de Bellocq, J.G and Morand, S. 2002. Mammal density and patterns of ectoparasite species richness and abundance. *Oecologia* **131:** 289-295

Statistics Norway (2009) *Official hunting statistics of Norway.* Statistics Norway, Oslo and Kongsvinger.

Toupin, B., Huot, J. and Manseau, M. 1996. Effect of insect harassment on the behaviour of the Riviere George Caribou. *Arctic* **49:** 375-382

The Norwegian Meteorological institute. 2010. Været i Norge 2009. The Norwegian Meteorological institute, Oslo, Bergen and Tromsø. [In Norwegian]

The Norwegian Meteorological institute. 2009a. Været i Norge 2008. The Norwegian Meteorological institute, Oslo, Bergen and Tromsø. [In Norwegian]

The Norwegian Meteorological institute. 2009b. Været i Norge klimatologisk månedsoversikt august 2009. The Norwegian Meteorological institute, Oslo, Bergen and Tromsø. [In Norwegian]

The Norwegian Meteorological institute. 2009c. Været i Norge klimatologisk månedsoversikt mai 2009. The Norwegian Meteorological institute, Oslo, Bergen and Tromsø. [In Norwegian]

The Norwegian Meteorological institute. 2009d. Været i Norge klimatologisk månedsoversikt april 2009. The Norwegian Meteorological institute, Oslo, Bergen and Tromsø. [In Norwegian]

Van Buskirk, J. and Ostfeld, R.S. 1995. Controlling Lyme disease by modifying the density and species composition of tick hosts. *Ecological Applications* **5:** 1133-1140

Vassallo, M., B. Pichon, J. Cabaret, C. Figureau, and C. Pérez-Eid, 2000. Methodology for sampling questing nymphs of *Ixodes Ricinus* (Acari: Ixodidae), the principal vector of Lyme disease in Europe. *Journal of Medical Entomology* **37:** 335-339.

Appendices

Appendix 1

Initial correlation test – GAM plot

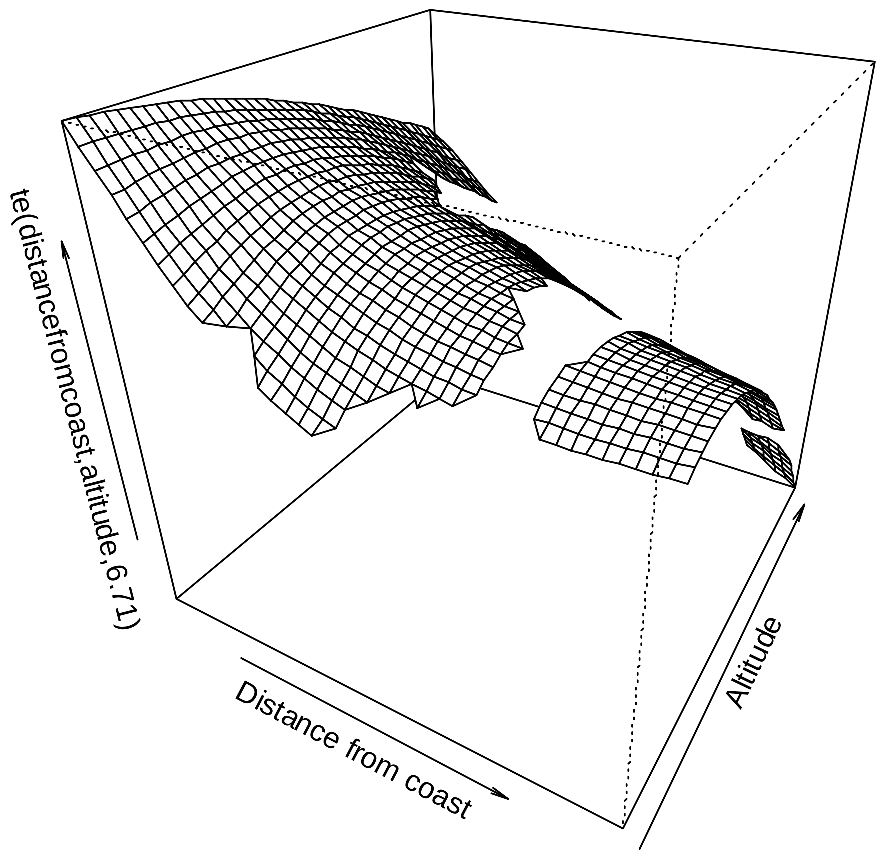


Figure 1. Generalised Additive Modelling (GAM), in the package mgcv in R, was used to check for linearity between the response and predictor variables. This GAM-plot showed an approximate linearity between tick abundance and distance from coast. There were, however, indications that altitude should be modelled with a 2nd order term. This is seen by the fact that the curve of the graph is slightly steeper at high altitudes and far away from the coast. Apart from this there seems to be no correlation between altitude and distance from the coast that would affect the results.

Appendix 2

Tick abundance in relation to altitude and distance from the coast

Analyses showed that a polynomial of third order gave the best fit of the data. Akaike information criterion (AIC), were the goal is to obtain the lowest AIC-value possible, was used to determine what polynomial that gave the best fit of a line to the points.

Table 1. AIC values for polynomials of altitude. I did only fit a third order polynomial because a graph of too high order would give the graph to much flexibility and would lead to small clusters, that will appear because of the design of the study, having a larger effect than they actually have.

	AIC	diff AIC	AICw
Altitude	3327.0	15.7	0.000
Altitude^2	3314.2	2.9	0.190
Altitdude^3	3311.3	0	0.810

Table 2. AIC values for polynomials of distance from coast. I did only fit a third order polynomial because a graph of too high order would give the graph to much flexibility and would lead to small clusters, that will appear because of the design of the study, having a larger effect than they actually have.

	AIC	diffAIC	AICw
Distance from coast	3337.8	37.5	0.000
Distance from coast^2	3310.4	10.1	0.006
Distance from coast^3	3300.3	0	0.994

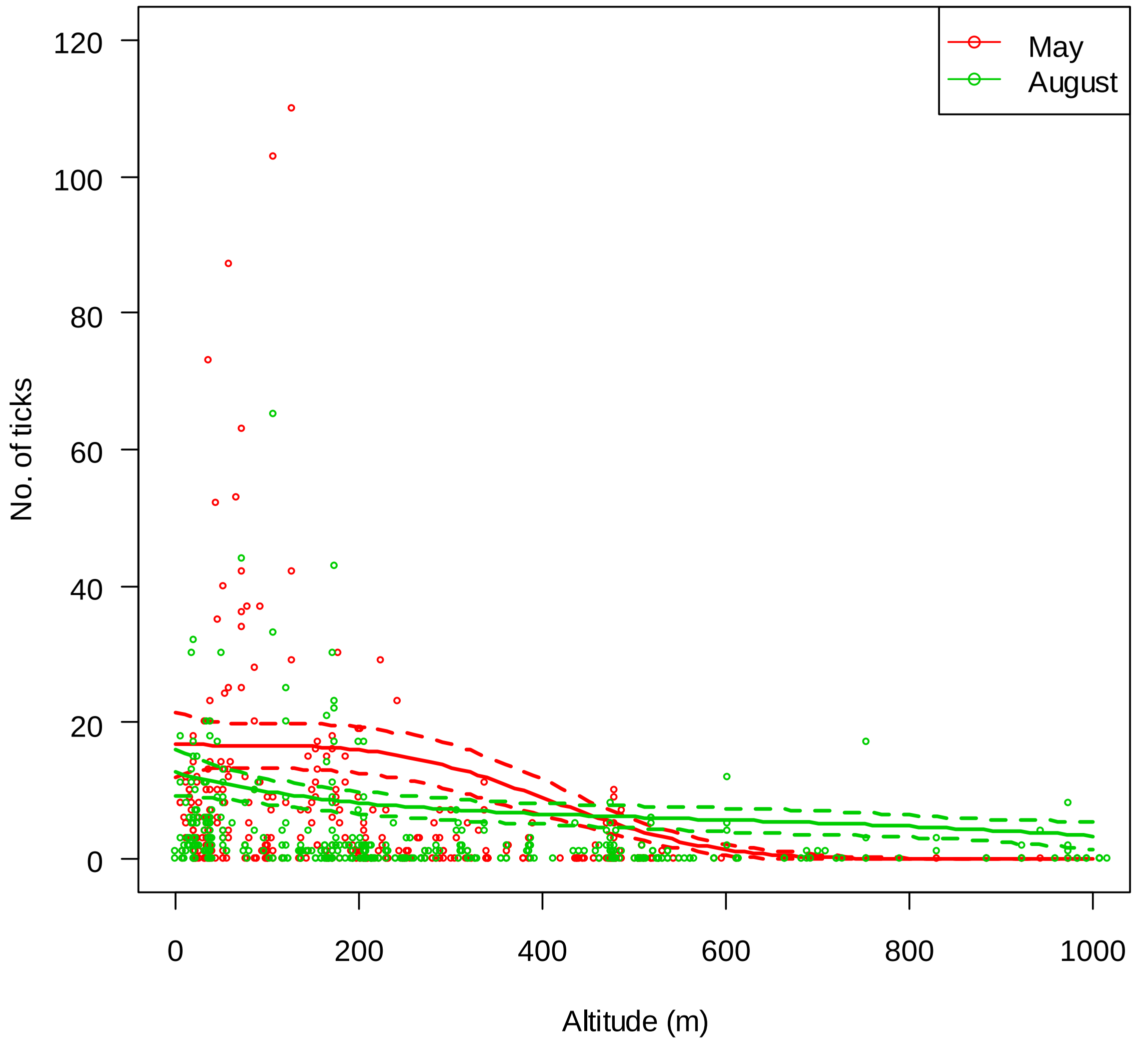


Figure 1. The same graph as in figure 4 with outliers.

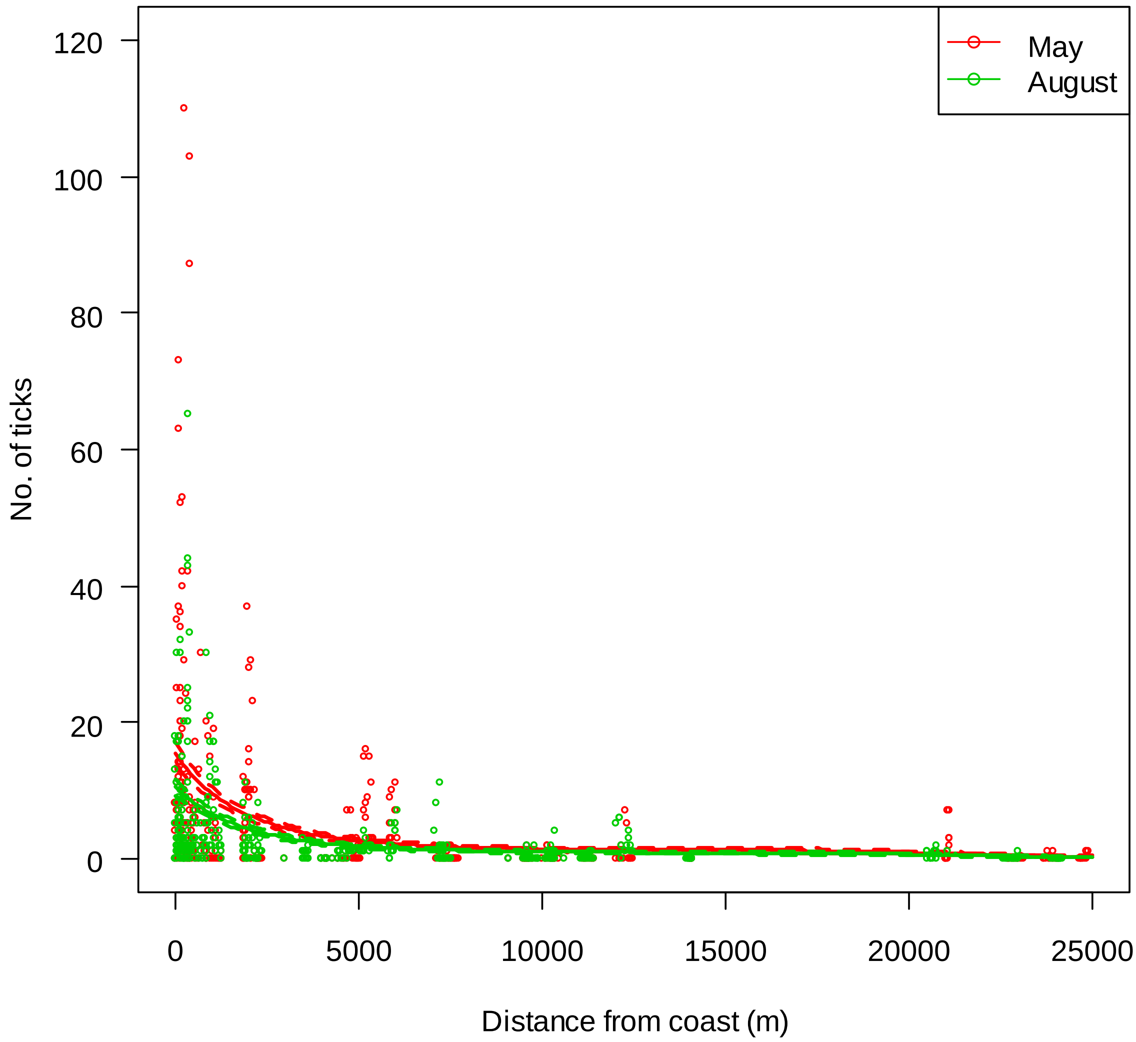


Figure 2. The same graph as in figure 5 with outliers.